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Seasonal change in factors affecting spatial microdistribution in a population of the satyrine butterfly *Lethe diana*

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Abstract The microdistribution of butterflies may be affected by food distribution, microclimatically favourable spots, or mate-locating sites. When butterflies' needs for these factors change, their microdistribution may change. In the satyrine butterfly *Lethe diana*, a multivoltine species, a seasonal change was observed in the factors that determine the microdistribution of adult butterflies. The microdistribution of every generation was mainly affected by the distribution of sap fluxes, resulting in a patchy butterfly population. The spatial arrangement of habitat patches also changed seasonally. Patches extended into the forest only for the July-August generation, due to seasonal changes in preferred light conditions. To avoid excessive increases in body temperature, the July-August generation of butterflies preferred dark sites within the forest. Generations from other months preferred more sunny sites, so their distribution was limited to near the forest edge. The microdistribution of males of the May-June generation was also affected by territoriality: territories were settled at relatively open sites along the forest edge.

Key words Microdistribution, seasonality, *Lethe diana*, sap flux, light-condition, territory.

Introduction

Animals are often contagiously distributed according to the influence of a variety of abiotic and biotic factors, such as the distribution of food, shelter, microclimatically favourable spots or intra- and interspecific interactions (Loertscher *et al.*, 1995). In butterflies, the distribution of food of both adult and larva is an important control on adult microdistributions (Ehrlich & Gilbert, 1973; Sharp *et al.*, 1974; Watanabe, 1978; Smiley *et al.*, 1988; Novotny *et al.*, 1991; Jordano *et al.*, 1992; Loertscher *et al.*, 1995; Brommer & Fred, 1999). The distribution of microclimatically favourable spots (Ravenscroft, 1994*a*; Dover, 1996) and mate-locating sites (Brakefield, 1982; Rutowski, 1991) are also thought to affect butterfly microdistributions. Therefore, resources and site characteristics are generally the determinant factors of butterflies' microdistributions. However, the requirements of butterflies may change seasonally. For instance, the Pipevine Swallowtail Butterfly, *Battus philenor*, switches oviposition plant seasonally (by switching search image) in response to host availability (Rausher & Odendaal, 1987). In such a case, the microdistribution changes accordingly.

In this paper, I studied seasonal change in the microdistribution of the satyrine butterfly *Lethe diana* (Butler). *L. diana* is a multivoltine species that inhabits woodlands in China, Korea, Sakhalin and Japan. Adults feed on sap exuded by wounded trees of various species, dung and dead animals (Fig. 1), and those of the first generation exhibit a territorial behavior (Fig. 2). Larvae feed on blades of various species of bamboo (Fukuda *et al.*, 1984). The purpose of this paper is to clarify the influence of these resources and favorable sites on the butterfly's seasonal microdistribution.

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Materials and methods

This study was performed at the Kamigamo Experimental Forest Station (Graduate School of Agriculture, Kyoto University), in the northern area of Kyoto City, Japan (Figs 3–4). A detail description of the habitat can be found in Ide (in press). In this area, *L. diana* larvae feed mainly on the bamboo grass *Sasa palmata* Nakai. *S. palmata* colonies lie scattered in this station (Fig. 5a).

Adults of *L. diana* appear twice a year in Kyoto: from May to mid-June and from mid-July to early October. The latter period actually produces two generations (Ide, unpublished data). In order to separate the two generations, the census data were divided into two groups, *i. e.*, those from July to August and those from September to October, for convenience sake in this paper. I call the three generations as the May–June generation, the July–August generation and the September–October generation, respectively.

To study the microdistribution of *L. diana*, mark-resight censuses were carried out on most days that the weather was fine during the adult season of 1999. Fixed forest routes were searched. Unmarked butterflies were captured with a soft insect net and numbered with a felt-tipped pen (green for males or red for females) on the undersurface of both hindwings. The butterfly was then released at the capture point immediately after its code number, sex,

Fig. 1. Two *Lethe diana* butterflies feeding on sap. Top is female and bottom is male.
Fig. 2. A male *Lethe diana* holding territory in the sunshine.
Figs 3–4. View of the study area.

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and location were recorded. When marked individuals were found, their code numbers and locations were recorded without capture.

Multiple regression analysis was carried out in order to test environmental factors affecting the microdistribution of *L. diana*. The mark-resight route was divided into 130 twenty-meter sections (Fig. 5b). Data on the following variables were analyzed for each section: the criterion variable was the total number of adults (captured or resighted), and the explanatory variables were the number of sap fluxes, whether bamboo grass was present or not in the section (present=1, not present=0), the number of territorial sites, and light-condition score. The light condition score follows Dover's (1996) insolation score, with modifications; it uses an aspect scale of 0–4, where open=4, south-facing=3, east- or west-facing=2, north-facing=1, and closed=0.

Results

Capture data

The numbers of butterflies marked of each sex and total abundance (sum of captures and resights) are shown in Table 1. The female-biased sex ratio in the September–October generation appears to be due to surviving females from the July–August generation that were captured in September and October because they emerged later than the males (Iwasa *et al.*, 1983; Sawada, 2000).

The number of captures and resights in each section in each generation is shown in Fig. 6. The distribution of *L. diana* was very contagious in every generation, but the densely populated sections changed seasonally. Many of the May–June generation butterflies (Fig. 6a) were captured and resighted at sections in the open field, and near bamboo grass in the northern area of the open field. For the July–August generation (Fig. 6b), many captures and resights were in dark sections among bushes and in the bamboo grass in the northern area of the open field, but butterflies were seldom captured or resighted at the sections in the open field. The distributed range of the September–October generation (Fig. 6c) was very limited at the sections near bamboo grass at the northern area of the open field, and few butterflies were captured and resighted in the dark bushes.

Distribution factor

The results of the multiple regression analysis are shown in Table 2. Any butterflies captured outside the research sections (2 males and 1 female of the July–August generation; 2 males of the September–October generation) were not included in this multiple regression analysis.

Table 1. Total number of captures (number of individuals in parentheses) and sex ratio of *Lethe diana*. Sex ratio is given by males/(males+females).

	MAY-JUN	JUL-AUG	SEP-OCT
Male	144 (73)	211 (133)	51 (36)
Female	76 (60)	116 (83)	85 (45)
Ratio	0.655 (0.549)	0.645 (0.616)	0.375 (0.444)

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Table 2. Factors affecting the microdistribution of *Lethe diana*.

		Explanatory variable	Standard regression coefficient	t	P	Cumulative r^2
MAY-JUN	Male	Constant	−1.048	−1.679	0.096	
		Sap flux	0.469	6.578	<0.001	0.203
		Territory	0.407	5.792	<0.001	0.382
		Light condition	0.105	1.477	0.142	0.393
		Bamboo grass	0.045	0.631	0.529	0.395
MAY-JUN	Female	Constant	−0.564	−1.403	0.163	
		Sap flux	0.491	6.261	<0.001	0.243
		Bamboo grass	0.101	1.304	0.195	0.255
		Light condition	0.090	1.148	0.253	0.264
		Territory	0.055	0.707	0.481	0.267
JUL-AUG	Male	Constant	1.379	2.182	0.031	
		Sap flux	0.390	4.861	<0.001	0.191
		Light condition	−0.166	−2.073	0.040	0.214
		Bamboo grass	0.144	1.814	0.072	0.234
		Territory	0.007	0.083	0.934	0.234
JUL-AUG	Female	Constant	0.765	2.150	0.034	
		Sap flux	0.368	4.675	<0.001	0.186
		Bamboo grass	0.219	2.809	0.006	0.226
		Light condition	−0.195	−2.487	0.014	0.264
		Territory	−0.024	−0.314	0.754	0.265
SEP-OCT	Male	Constant	−0.505	−1.912	0.058	
		Sap flux	0.566	7.640	<0.001	0.186
		Light condition	0.098	1.334	0.185	0.331
		Bamboo grass	0.093	1.266	0.208	0.340
		Territory	0.087	1.186	0.238	0.348
SEP-OCT	Female	Constant	−1.171	−1.881	0.062	
		Sap flux	0.556	7.368	<0.001	0.307
		Light condition	0.089	1.189	0.237	0.316
		Bamboo grass	0.073	0.972	0.333	0.322
		Territory	0.006	0.079	0.937	0.322

The standard regression coefficients for the distribution of sap fluxes were the largest in every generation, although r^2 values were generally small. The distribution of territorial sites only explained the distribution of males in the May-June generation. The light-condition score correlated with neither the May-June nor the September-October generation, and negatively correlated with the July-August generation. The sap flux distribution therefore appears to be the main control on the microdistribution of these butterflies.

To examine the influence of sap fluxes on the movement of butterflies, the proportion of resights in the same section was compared between sections with sap fluxes and those without (Fig. 7). Butterflies released in sections with sap fluxes were resighted in the same section more frequently than those released in sections without sap fluxes, with the exception of the

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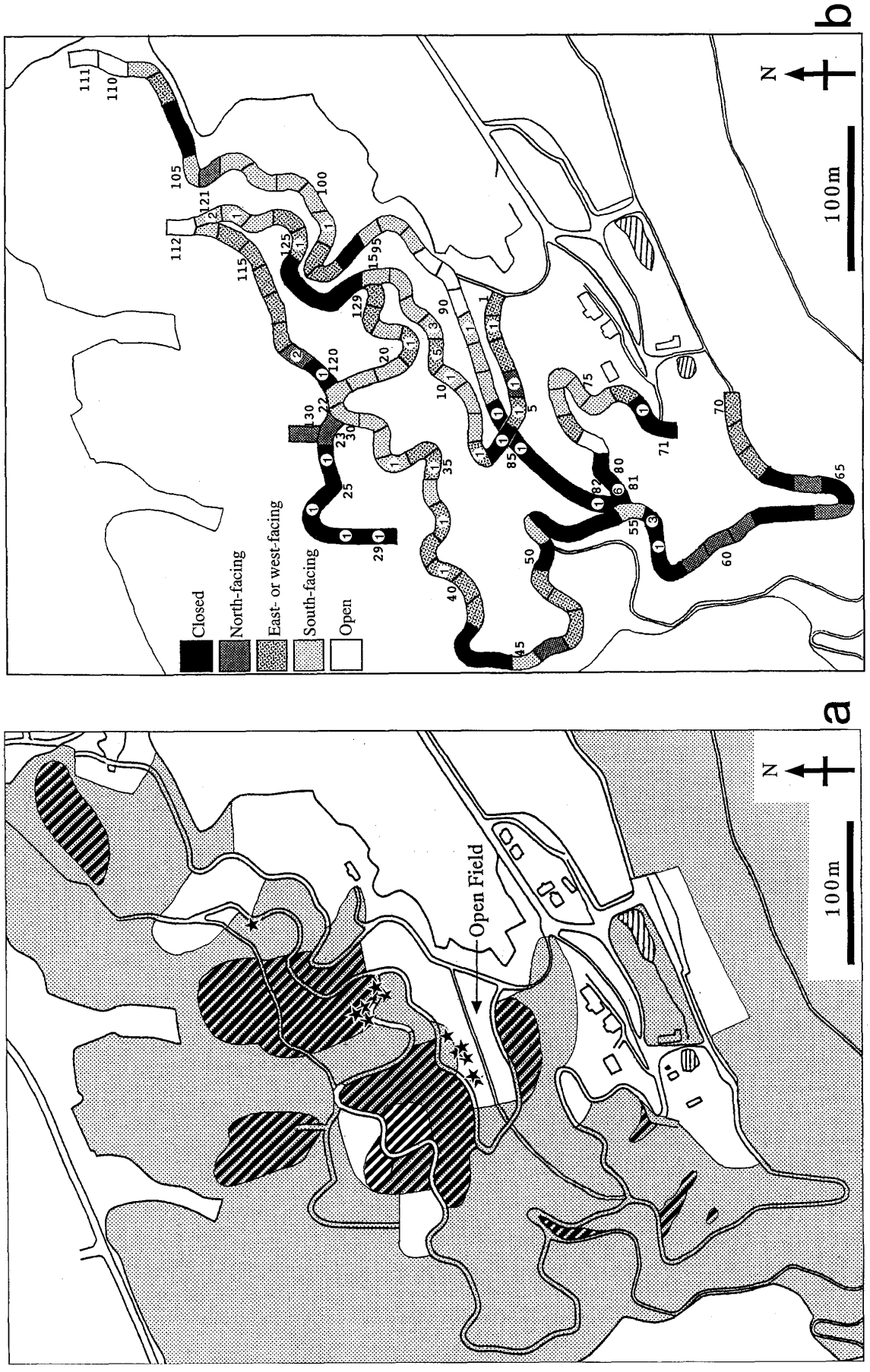

Fig. 5. Map of study area. a) Map showing woods (stippled area) and bamboo grass colony (diagonal lined area). Stars indicate points where territorial behavior was observed. b) Map showing mark-resight census route and sections. Patterns of sections indicate their light-condition score. The numerals in circles indicate number of sap fluxes in the section.

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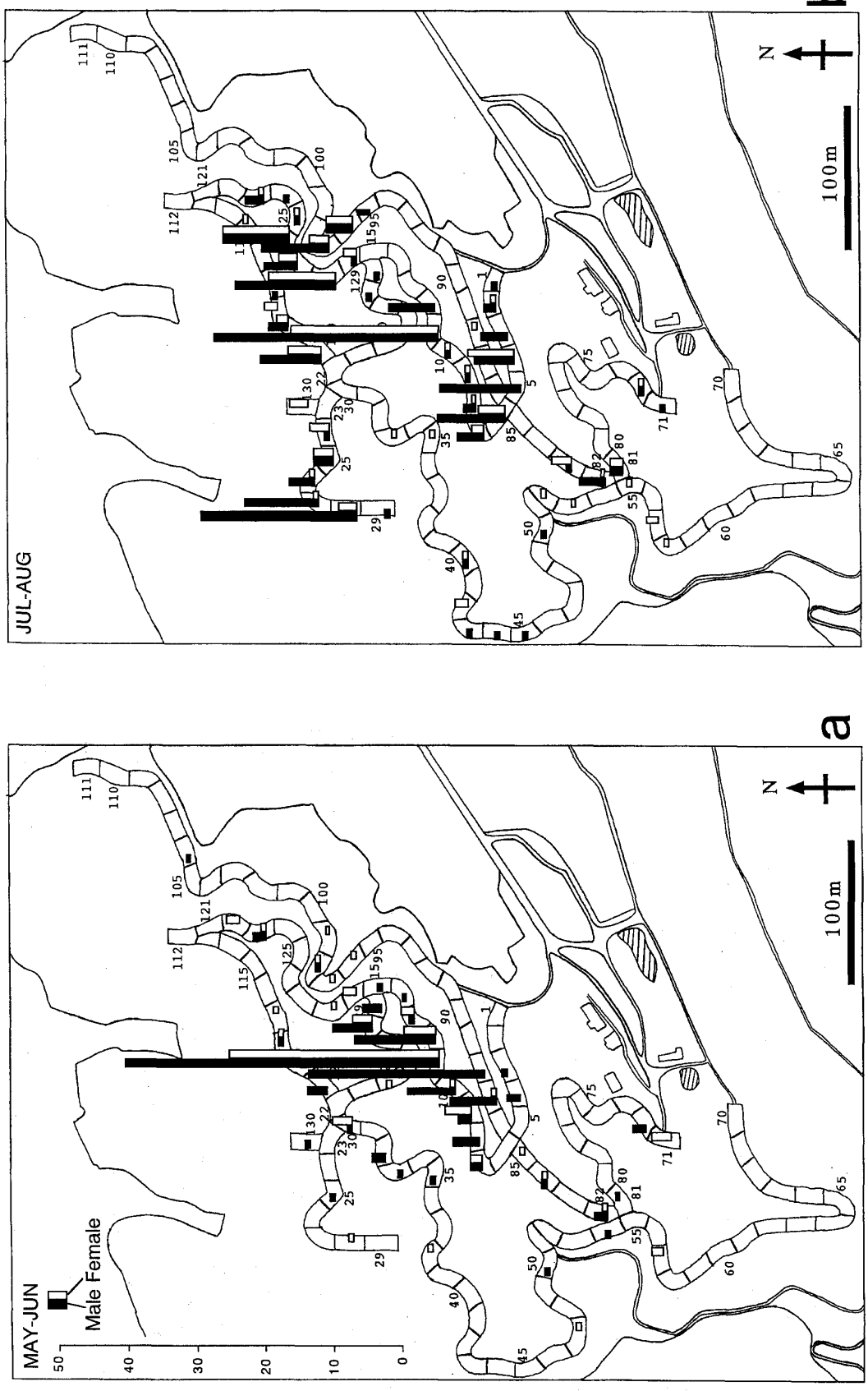

Fig. 6. Distribution of *Lethe diana*: a) May–June generation, b) July–August generation, c) September–October generation. Butterflies of the May–June generation were captured mainly in the open field (sections 87, 88) and near the bamboo grass in the northern areas of the open field (sections 10, 11, 12). The July–August generation was captured in dark bushes (sections 5, 6, 7; 25, 26, 27, 28; 96, 97, 126, 127, 128), as well as in the bamboo grass colonies in the northern areas of the open field. Butterflies of the September–October generation were concentrated near the bamboo grass in the northern area of the open field (sections of 11, 12).

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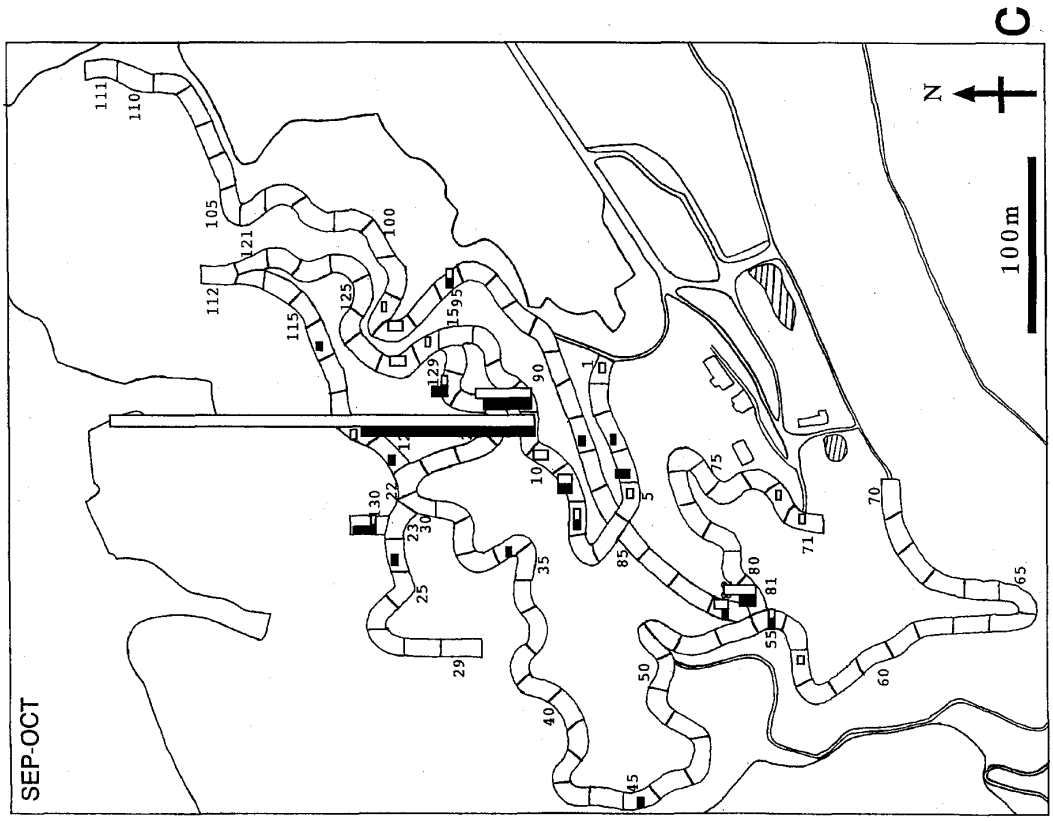

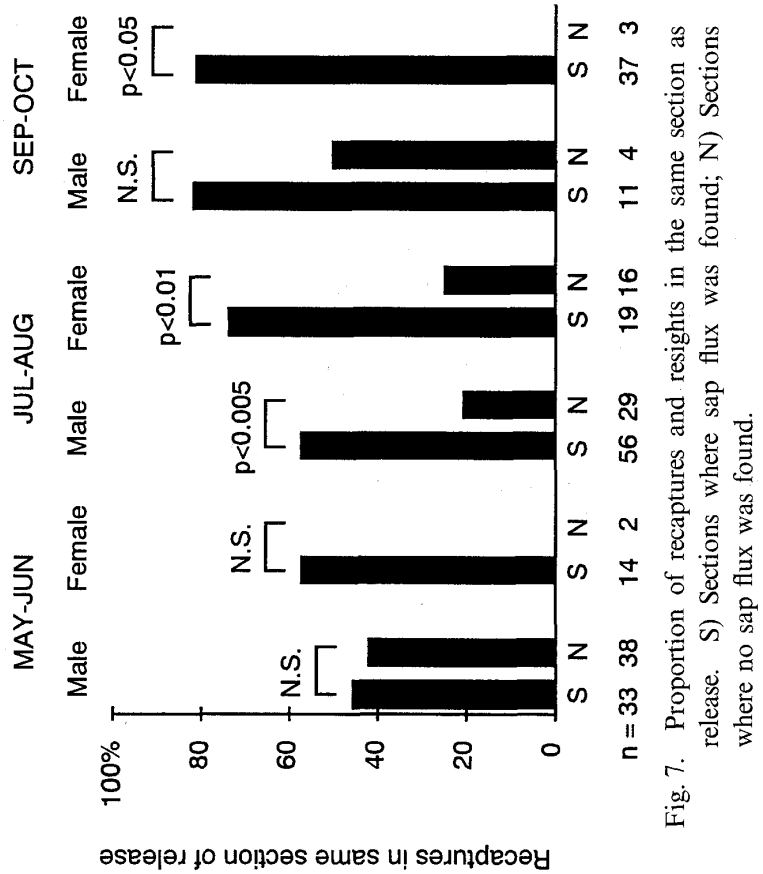

Fig. 7. Proportion of recaptures and resights in the same section as release. S) Sections where sap flux was found; N) Sections where no sap flux was found.

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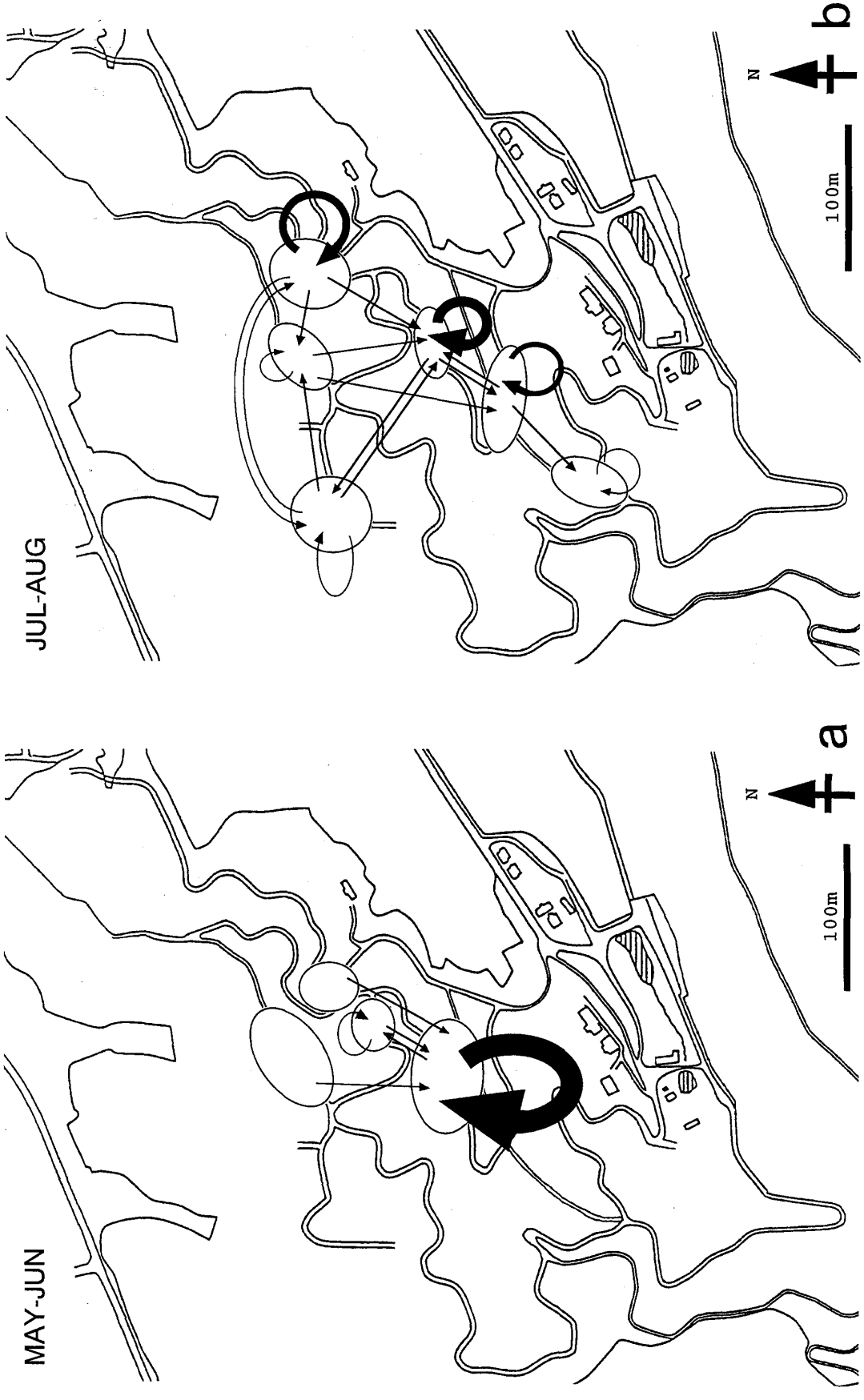

Fig. 8. Arrangements of habitat patches and movements of butterflies between patches. a) May–June generation, b) July–August generation, c) September–October generation. The width of arrows indicate the number of butterflies recaptured in the same patch or different patches.

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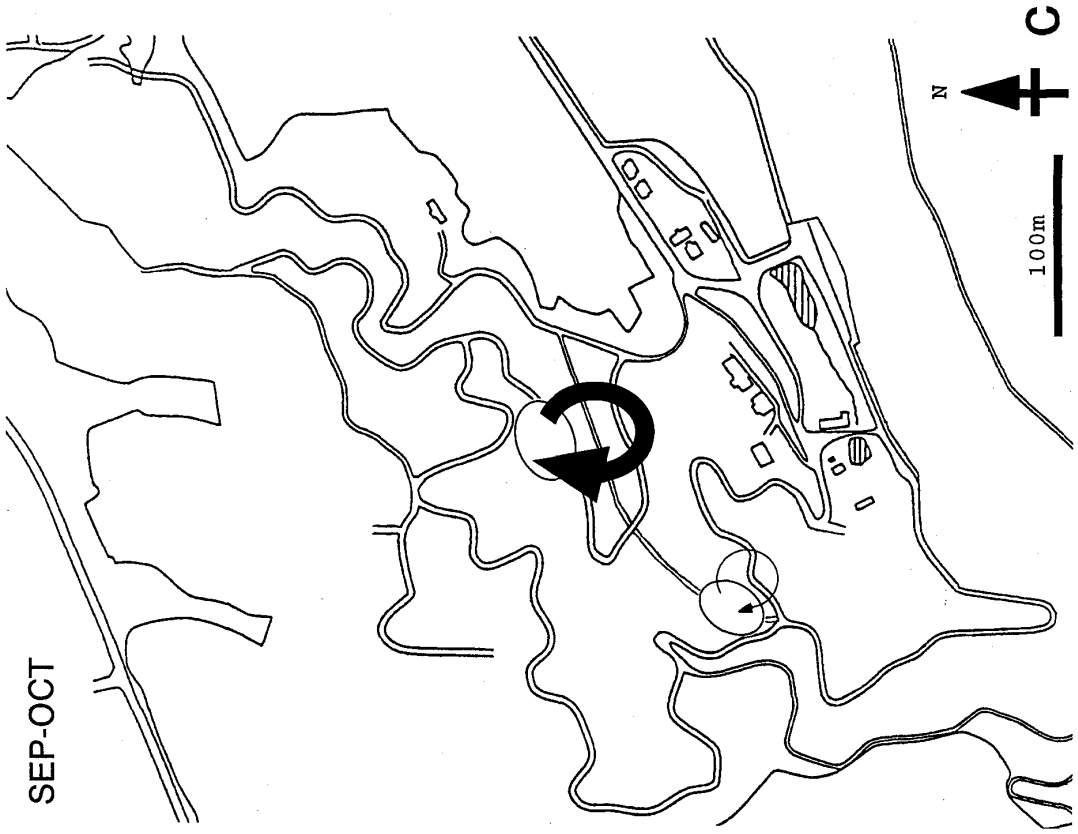

May-June males. In the May-June females and the September-October males, there were no significant differences between sections with or without sap fluxes in the proportion of resights in the section of release (Fisher's exact probability test). However, this was because few butterflies were found in locations lacking sap fluxes, and therefore few were released there. In the May-June males, the proportion of resights in the same section was not significantly higher in sections with sap fluxes than in those without, but when the comparison was controlled for the effect of territorial sites, there was a positive relationship between resights and sap fluxes ($p<0.05$). Thus, butterflies remained around sites with sap fluxes and deserted sites without, so they became contagiously distributed around sites with sap fluxes.

Discussion

Many authors have reported that the distribution of nectar sources determines the microdistribution of butterflies (*e. g.* Murphy *et al.*, 1984; Loertscher *et al.*, 1995; Dover, 1996). On the other hand, it has also been reported that fewer butterflies were distributed around host plants of larvae (Ravenscroft, 1994*b*). In *L. diana*, the distribution of sap fluxes (adult food) strongly correlated with their microdistribution in every generation, whereas the distribution of bamboo grass (the host plant of the larvae) barely correlated with that of the butterfly population. This resulted from *L. diana* remaining at sites with sap fluxes longer than at those without. Fig. 8 shows habitat patches, the sites where sap fluxes were found and butterflies were contagiously distributed. Movements between patches were observed and hence a patchy population (Harrison, 1991) based on the distribution of sap fluxes was formed.

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The arrangement of patches and the movement of butterflies between patches changed seasonally. Patches extended spatially and movement between patches became frequent in July–August; however patches were limited to small areas around the forest edge in May–June and September–October. The different microdistributions were probably the result of different factors in each generation.

The light-condition score was negatively correlated only with the butterfly microdistribution of July–August. This illustrates that butterflies are distributed at dark, shaded sites in summer. Butterflies are ectothermic animals; they generally regulate their body temperature by utilizing suitable thermal environments (Ohsaki 1986, 1996; Ravenscroft 1994*a*; Rutowski *et al.*, 1994). In *L. diana*, this thermoregulation behavior is evident in their preference for areas with lower light intensity in summer, to avoid excessive increases in body temperature (Ide, in press). Thus, in the hottest part of the summer, they utilize dark regions in forests and disperse widely, spatially extending their population distribution. Under the cooler conditions of late spring and early autumn, they raise their body temperature by congregating at sunny sites along the forest edge.

The microdistribution of the May–June males was correlated with territorial sites. In May–June, territories were settled at the sunny tips of branches that faced open space (Ide, in preparation), which made the forest edge the preferred area for settlement. The microdistribution of females was not correlated with territorial sites, because they leave a territory immediately after copulation to avoid harassment from males (Wiklund & Åhrberg, 1978; Baughman *et al.*, 1988; Odendaal *et al.*, 1989; Baguette *et al.*, 1996).

Among the determining factors of *L. diana* microdistributions, sap fluxes were a constant requirement, whereas light requirements changed seasonally. Consequently, the microdistribution also changed seasonally. When requirements of butterflies change, the spatial distribution of the determinant factors (*i. e.*, resources and favourable sites) also changes. The dispersal of butterflies is a function of the spatial distribution and the use of resources and of favorable sites (Gilbert & Singer, 1973; Brommer & Fred, 1999). Then, dispersal pattern of *L. diana* possibly change seasonally.

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摘　　要

クロヒカゲの局所的分布を決定する要因の季節変化 (井出純哉)

蝶のハビタット内での分布は成虫と幼虫の餌や微気象，配偶行動を行う場所などの影響を受けて決まると考えられてきた．これらの分布を決定する要因に対する蝶の好みが変化する場合，蝶の分布も変化することが予想される．そこでクロヒカゲ (鱗翅目; ジャノメチョウ亜科) を材料に，ハビタット内での成虫の分布を決めている季節ごとの要因を調べた．クロヒカゲは京都では年3化したが，世代にかかわらず成虫の餌である樹液資源の分布が最も強く影響しており，樹液が多く出ている場所を中心にしたパッチ個体群が形成されていた．パッチの空間配置は世代ごとに少しずつ変化し，5-6月と9-10月の世代は林縁部を中心に分布したが，7-8月の世代は林内に分布を広げていた．7-8月の世代は日当りの悪い場所に分布する傾向があったことから，世代ごとの分布の変化は7-8月の世代が体温上昇を抑えるために暗い場所を利用し，他の世代は体温を上げるために明るい場所を利用する結果と考えられた．また，5-6月の世代だけがなわばり行動を行うため，この世代の雄はなわばり行動を行う場所に分布が規定されていた．なわばり行動は前方が開けた木の梢で行われるため，5-6月の世代はなわばり行動を行うのに好適な場所が多い林縁部に分布する傾向を強めていると考えられた．

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